

abaxial or adaxial nectariferous gland often present; style usually 2-lobed, stigmatic lobe generally subapical, thin membranes borne on both sides of the style between or at the junction of the two lobes. Cleistogamous flowers of \pm similar morphology borne on basal, rarely aërial, branches in a few. Fruit a 2-loculate, glabrous [or pilose], thin-walled, loculicidal [sometimes winged] capsule, often accompanied by the persistent calyx. Seeds ovoid, globose, or ampulliform, pubescent, rarely glabrous and finely tuberculate, usually bearing a 2- or 3-lobed aril at the micropylar end [a hilar appendage present in some]; cotyledons ovate or linear, endosperm continuous, fleshy. (Including *Asemeia* Raf., *Galypola* Nieuwl., *Pilostaxis* Raf., *Senega* Spach, *Triclisperma* Raf.). LECTOTYPE SPECIES: *P. vulgaris* L., see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 446. 1913. (A pre-Linnaean name from Greek, *polys*, much, and, *gala*, milk, in reference to a plant which was thought to increase lactation.) — MILKWORT.

A large (about 500 species), widely distributed genus (throughout Temperate and Tropical Zones, but absent from New Zealand, Polynesia, and the Arctic regions), well known for its small, usually brightly colored flowers. In North America the genus is best represented in the eastern part of the continent and in the southwestern United States and Mexico. It is largely absent from the dry, mid-continent region and the Pacific Northwest (*Polygala californica* Nutt. ex Torr. & Gray from central, coastal California to southwest Oregon only). Blake (1924) credits 31 species to the southeastern United States; Small (1933) accepts 37 species (in five genera) for the same area. Many are endemic to parts of this region; others occur northward or in the Caribbean region where the genus is also well represented.

In his *Monographia Polygalacearum*, Chodat (1893) proposed dividing *Polygala* into ten sections.² One of these has been renamed sect. PSEUDO-SEMEIOCARDIUM Adema, a change necessitated by the demonstration that the type of sect. SEMEIOCARDIUM (Zoll.) Chodat (*Semeiocardium Ariensii* Zoll., which occurs on Madura and Kangean islands off northeast Java) is actually a member of the Balsaminaceae (see C. A. Backer,

² While unambiguously using the rank *sectio* in the monograph, Chodat refers to several of the sections as *sous-genres* in at least one prior (1889) and one subsequent (1913) work. However, there is no definite indication that he intended to use subgenus in the formal sense that it is now employed. Indeed, since *sous-genre* and *sectio* are freely interchanged on pp. 154 and 155 in the 1913 paper, they seem to have been employed as equivalent categories, as A. P. de Candolle and others had used them earlier (see G. K. Brizicky, *Taxon* 18:643-660. 1969).

layer of seed coat hatched (semidiagrammatic), $\times 8$; k, branch bearing two young capsules developed from cleistogamous flowers, $\times 2$; l, cleistogamous flower, perianth and androecium pulled away from style (see text), $\times 10$. m-p, *P. grandiflora*: m, flower at anthesis, $\times 6$; n, flower in lateral view, one sepal (wing) and part of the corolla removed, $\times 6$; o, fruit in lateral view, one sepal (wing) removed, $\times 6$; p, arillate seed, $\times 10$.

Gard. Bull. Singapore 9: 70-72. 1 pl. 1935). Blake's classification (1916) in which many of Chodat's sections are treated as subgenera expresses the morphological diversity of the genus better. In the region covered by the *North American Flora*, Blake (1924) later recognized 13 infrageneric categories (including *Badiera* DC., subshrubs with subequal sepals, predominantly of West Indian distribution) whose rank, unfortunately, was not indicated.

Species belonging to three subgenera are found in the southeastern United States. Only one member of subg. CHAMAEBUXUS (DC.) Blake (keel cristate, calyx caducous, abaxial sepals separate), *Polygala paucifolia* Willd., fringed polygala, flowering wintergreen, occurs in our area or elsewhere in eastern North America, although species assigned to this subgenus are known from the southwestern United States. A plant of wide but somewhat sporadic distribution, typically found in moist, deciduous forests, this species ranges from Quebec (Anticosti Island and Gaspé County), southward through parts of New England, New York, and Pennsylvania and along the mountains to northern Georgia (including a few stations in western North and South Carolina and eastern Tennessee). It extends westward across southern Ontario (as far north as James Bay), Michigan, northern Wisconsin, and Minnesota to southern Manitoba and central Saskatchewan.

Differing from our other species of *Polygala* in having six rather than eight stamens, an obscurely bilobed stigma lacking a tuft of hairs, an adaxial nectariferous gland, and seeds with three-lobed arils, *P. paucifolia* appears to be closely related to certain other members of the subgenus, particularly the European *P. Chamaebuxus* L. In *P. paucifolia*, minute cleistogamous flowers are produced on short, erect branches that originate near the base of the upright leafy shoot (see FIGURE 1, a, k, l) and less frequently, later in the summer following disappearance of fruits developed from the chasmogamous flowers, at the apex of the plant or from axils of reduced leaves along the leafy shoot. While agreeing in general structure with the chasmogamous flowers, those of the cleistogamous type have a downward flexed, shortened style with an obviously two-lobed stigma, lack a crested keel, and have their stamens fused into two groups of three each, one unit borne on either side of the ovary and free from the corolla. Leaf-bearing branches of *P. paucifolia* overwinter and are replaced in the spring with foliage developing on a new shoot produced from the shallow rhizome.

Subgenus HEBECLADA (Chodat) Blake (keel ecristate, calyx persistent in fruit, abaxial sepals connate) is represented with us by *Polygala grandiflora* Walt., $2n = 28$, which ranges along the Coastal Plain (rarely at Piedmont localities) from southeastern North Carolina to Florida and westward to Mississippi. Members of this subgenus occur otherwise in South and Central America and in the West Indies. Specimens referable to *P. grandiflora*, particularly from southern Florida, vary greatly in leaf shape, flower color, and vesture. Several varieties have been distinguished in this region (see Blake, 1924), including var. *angustifolia* Torr. & Gray,

with linear or narrowly linear-lanceolate leaves (*vs.* narrowly lanceolate to elliptic in var. *grandiflora*, which probably includes *P. cumulicola* Small and *P. miamiensis* Small, both described from collections made in Dade County, Florida) and var. *leiodes* Blake, with glabrous or sparsely pubescent, linear leaves and sepals lacking nonglandular hairs. While accepting these varieties, Long stresses dark purple wings (*vs.* greenish or purplish in the others) as the distinguishing character of var. *leiodes*. These characters are often difficult to correlate in herbarium specimens, and the *P. grandiflora* complex in Florida remains perplexing and in need of further study.

Our other species, about 30 in number, belong to subg. POLYGALA (subg. *Orthopolygala* (Chodat) Blake, keel cristate, calyx persistent in fruit, abaxial sepals separate), which contains at least three-quarters of the species in the entire genus. Although Chodat (1893) provides a lengthy classification of the species in his sect. ORTHOPOLYGALA, some of the categories adopted appear unnatural (e.g., "Senegae," containing *Polygala Senega* L. and *P. polygama* Walt.), while others contain clearly related species (e.g., "Decurrentes," comprised of *P. lutea* L., *P. Rugelii* Shuttlw. ex Chapm., *P. nana* (Michx.) DC., *P. cymosa* Walt., *P. ramosa* Ell., and *P. Balduinii* Nutt.). Small (1933), treating only those species found in our area, recognized a monotypic genus, *Galypola* Nieuwl., for *P. incarnata* L., *Pilostaxis* Raf. for species in the Decurrentes, and kept the residuum in *Polygala* in which seven informal, although named, categories were presented. The characters used to distinguish the two genera are minor and seem better utilized at some infrageneric rank.

Eight, possibly more, endemic species belonging to subg. POLYGALA occupy portions of the Southeast. Known only from Florida are *Polygala Lewtonii* Small, with cleistogamous flowers, according to Blake (1924), reported from the sandy *Pinus clausa* scrub areas in the central part of the state (Highlands, Lake, Marion, Orange, and Polk counties) and *P. Rugelii*, $2n = 68$, which grows on wet, sometimes peaty sands throughout the Florida peninsula. Others, less restricted in distribution, and found mainly at places along the Coastal Plain, include *P. Balduinii* Nutt. (possibly conspecific with *P. Carteri* Small, from southern Florida, but this problem needs further study), *P. setacea* Michx., *P. crenata* James, with cleistogamous flowers borne on basal, leafless branches, *P. Chapmanii* Torr. & Gray, $2n = 72$, *P. leptostachys* Shuttlew. ex A. Gray, *P. Boykinii* Nutt. var. *Boykinii*, $2n = \text{ca. } 28$, and from south Florida only, *P. Boykinii* var. *sparsifolia* Wheelock (which probably includes *P. flagellaris* Small and is presumably the same as *P. praetervisa* Chodat, $2n = 96$, since the types cited by Wheelock and Chodat are portions of the same collection).

The more widespread, nonendemic species have ranges of several types. Occurring predominantly outside of the Southeast and found in various parts of this region are *Polygala leptocaulis* Torr. & Gray, a plant of damp meadows and low pinelands in Florida, Mississippi, and Louisiana, which otherwise occurs in Texas, parts of Central and South America, and at

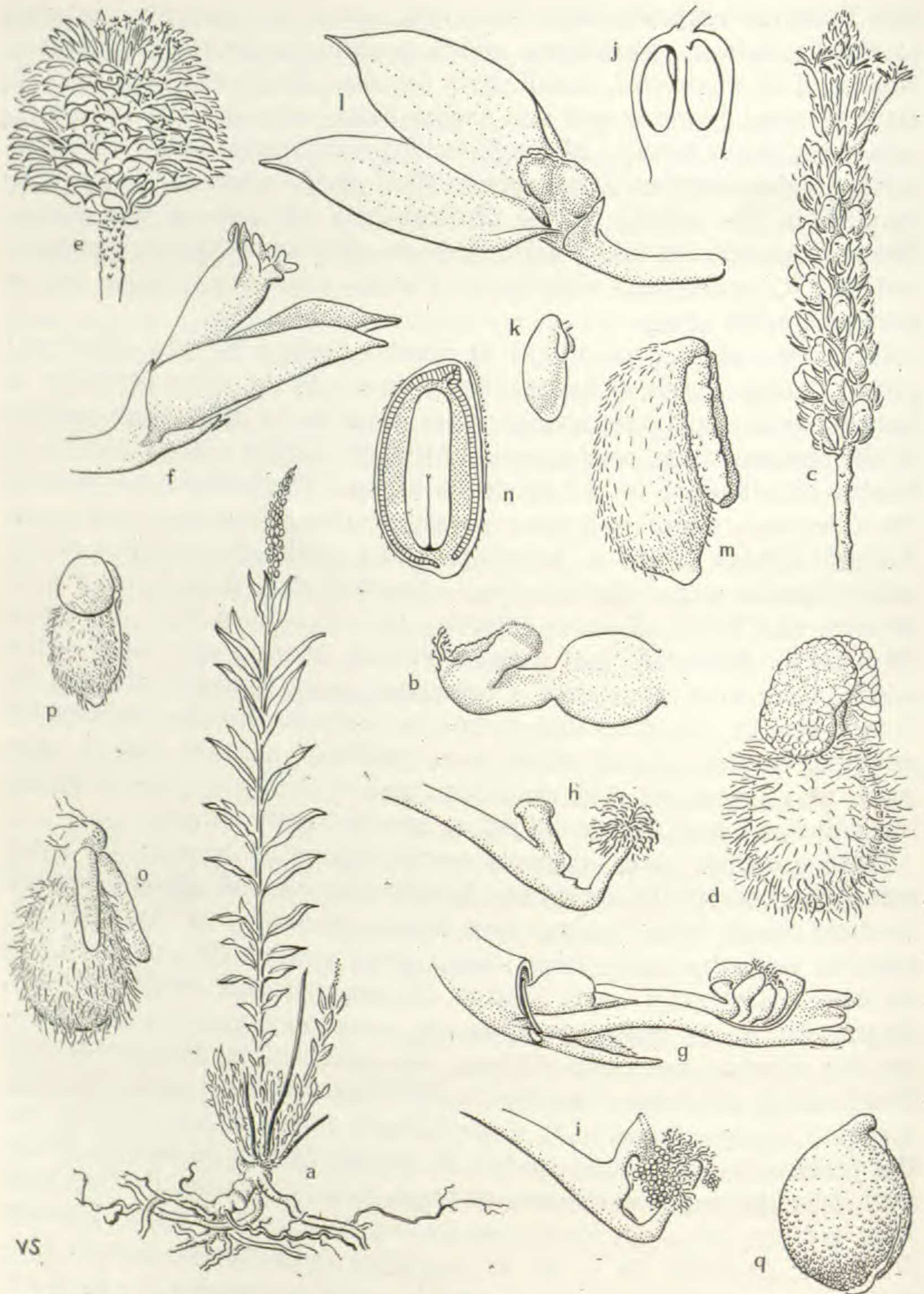


FIGURE 2. *Polygala* subg. *Polygala*. a, b, *P. Senega*: a, habit of plant in flower, all mature stems except one removed, $\times 1/3$; b, gynoecium from flower at anthesis, $\times 20$. c, d, *P. incarnata*: c, inflorescence, flowers near the apex, fruits toward the base, $\times 1\ 1/2$; d, seed with two-lobed aril, $\times 15$. e-n, *P. lutea*: e, inflorescence, flowers near the apex, fruits toward the base, $\times 1\ 1/2$; f, flower, $\times 8$; g, flower in lateral view just prior to anther dehiscence showing arrangement of stamens about apical brush, perianth mostly removed, $\times 12$; h, style apex with stalked stigma and brush from flower at same stage as that in g, $\times 25$; i, style apex from older flower, stalked stigma bent toward the apical brush which collects the pollen, $\times 25$; j, ovary in slightly oblique longitudinal sec-

places in the West Indies, and *P. alba* Nutt., $2n = 24$, ca. 72, and 104–108, which Blake (1924) credits to Louisiana and Wheelock to Arkansas, although specimens have been seen only from the region to the west (Puebla, Mexico, to Texas and Arizona, and northward to southern Saskatchewan). Other species of less restricted distribution in the Southeast, but which nevertheless occur mainly beyond our area, are *P. Senega* L., known primarily from calcareous sites from northern Maine across Ontario (north to the James Bay region) to western Alberta, and south to the Carolinas, Georgia, Tennessee, Arkansas, and South Dakota; *P. sanguinea* L., from Nova Scotia to southern Ontario and Minnesota, south to North Carolina, Tennessee, Alabama, Louisiana, Mississippi, and eastern Texas; and *P. verticillata* L. var. *verticillata* (*P. Pretzii* Pennell),³ which ranges widely throughout the eastern United States and southern Canada south to Tennessee (Pennell, 1931) and Louisiana. Several varieties (some often treated as species) are usually recognized as distinct from var. *verticillata*. Those represented in our region (and also to the north) include *P. verticillata* var. *isocycla* Fern. (*P. verticillata* L. var. *verticillata* sensu Pennell), $2n = 34$, a plant of dry soils throughout the Southeast, *P. verticillata* var. *ambigua* (Nutt.) Wood, from North Carolina to Arkansas, at stations mostly inland from the Coastal Plain, and *P. verticillata* var. *dolichoptera* Fern., from Arkansas.

A second group of species, growing chiefly in savannahs or on wet, often peaty sands, ranges widely across the Gulf and Atlantic coastal plains, sometimes occurring west to eastern Texas and north to coastal New England. These are *P. Hookeri* Torr. & Gray, from North and South Carolina, Florida, and Louisiana (to Texas, Blake, 1924); *P. brevifolia* Nutt., from New Jersey, North Carolina, Florida, Alabama, and Mississippi; *P. nana* (including *P. arenicola* Small), $2n = 68$, from South Carolina (Lexington Co.) and Tennessee (Rhea Co.), Georgia, Florida (widespread), west to Louisiana, eastern Texas (and Arkansas, Blake, 1924); *P. ramosa*, $2n = 68$, from New Jersey (Small, 1933) and Delaware to Florida, west to eastern Texas; *P. cymosa*, from Delaware to Florida, west to eastern Louisiana; and *P. lutea* (with orange, rarely yellow flowers), $2n = 68$, from Long Island to Florida, west to eastern Louisiana.

The third group, species found both at Coastal Plain localities and more or less widely in the interior of the continent, includes the following: *P. polygama* Walt. (including *P. aboriginum* Small, according to James),

³ See Fernald (1938) and Pennell (1933 & 1939) for two different views on the interpretation of the Linnaean type of this species.

tion, at left, ovule with immature aril, at right, ovule showing funiculus (semi-diagrammatic), $\times 20$; k, ovule with immature two-lobed aril, $\times 25$; l, fruit and persistent calyx, corolla fugacious, $\times 6$; m, seed with two-lobed aril, $\times 25$; n, seed in longitudinal section, endosperm stippled, inner layer of seed coat hatched (semi-diagrammatic), $\times 25$. o, *P. nana*, arillate seed, $\times 25$. p, *P. ramosa*, arillate seed, $\times 25$. q, *P. cymosa*, seed, aril minute or wanting, $\times 25$.

$2n = 56$, with aërial (Robinson, Shaw) or subterranean racemes of cleistogamous flowers, distributed from Nova Scotia to Florida, west to Texas, and at scattered localities inland on dry sandy soils from southern Ontario to Minnesota, south to Arkansas and northern Georgia (northern and inland material often referable to var. *obtusata* Chodat, $2n = 56$); *P. incarnata* L. (*Galypola incarnata* (L.) Nieuwl., our only species with the corolla at least twice as long as the wings), from Long Island to Florida, west to Texas, and inland sporadically to Wisconsin, Iowa, Kansas, and Oklahoma; *P. cruciata* L. (including *P. ramosior* (Nash ex Robinson) Small), $2n = 36$, with a distribution pattern similar to the preceding species, except inland (lake margins, meadows, peaty soils) to only the Upper Great Lakes region (Minnesota, Wisconsin, Michigan), and southward at scattered places in Illinois, Indiana, Ohio, Kentucky, Tennessee, and Alabama (most collections from the north, both coastal and inland, are referable to var. *aquilonia* Fern. & Schub.); *P. Curtissii* A. Gray, $2n = 40$, from Delaware to Georgia and Alabama, but less frequent southward along the Coastal Plain, although occurring inland from northern Alabama and Georgia, north to Ohio and West Virginia; *P. Nuttallii* Torr. & Gray, $2n = 46$, from Massachusetts south to North Carolina and Georgia, inland to Tennessee and Kentucky (also Alabama, Mississippi, and Arkansas, Blake, 1924, Small, 1933); and *P. mariana* Mill. (possibly including *P. Harperi* Small, which according to Fernald, Gray's Man. Bot. ed. 8. 956. 1950, ranges from southeastern Virginia to Florida, west to eastern Texas), $2n = 34$, from New Jersey to Florida, west to eastern Texas, Arkansas, and Tennessee.

Relatively little recent work on the anatomy and morphology of the genus has appeared. Holm mentions the occurrence of lysigenous oil ducts and oil drops in cortical and epidermal cells and discusses briefly certain other aspects of vegetative structure for some of the species found in our region. The morphology of the style and stigma, which varies somewhat from the basic two-lobed situation among the species studied by Holm, seems constant enough within certain groups of species to be useful in developing a future infrageneric classification. Anther walls in several Indian species (Venkatesh) are comprised of epidermal, hypodermal, middle, and tapetal layers. Cells of the hypodermis have fibrous bands that originate from a common point on the inner tangential wall, extend along the radial walls to terminate on the outer tangential wall. Shrinkage of the fibrous cells ruptures the anther wall in a predetermined zone on its inner, subapical surface. The occurrence of partially or entirely tetrasporangiate stamens in individual flowers of certain species indicates that the bilocular stamens of *Polygala* are derived by suppression of the two abaxial microsporangia.

The pollination mechanism in species of *Polygala* is an interesting but little studied subject. Venkatesh's work indicates that autogamy may commonly occur. In the Indian species investigated, self-pollination is facilitated by a curving of the style which brings the stigma into close contact with the pollen that accumulates in a special pocket on the style.

However, whether these species are proterogynous or proterandrous, and therefore suited to cross-pollination as well, was not mentioned. In many of our species self-pollination seems to occur also but by a somewhat different mechanism. For example in *P. lutea*, the apical stigmatic lobe ends in a tuft of hairs which catches pollen shed from the eight tightly surrounding anthers (FIGURE 2, g). At this stage the stigmatic lobe is bent away from the pollen mass and toward the base of the style (FIGURE 2, h). Later, as the flower ages, the stigmatic lobe is reoriented so that the stigmatic surface is presented to the accumulated pollen (FIGURE 2, i). Within a single flower, however, the relationship between the time of anther dehiscence and the period of stigma receptivity is not known precisely, so it is possible that the stigma is receptive at the time pollen is shed, and autogamy occurs only if cross-pollination by insects has not. Observations on living plants need to be made.

The relatively large flowers of *Polygala paucifolia*, in contrast, seem especially suited to bee pollination, which has been described for the related *P. Chamaebuxus* (Faegri & van der Pijl). The two lateral, petaloid sepals and the keel of these species (and other members of the Polygalaceae) are analogous to the wings (alae) and standard (vexillum) of papilionaceous legumes, and the pollination mechanism in certain members of both families has much in common. A bee in search of nectar produced at the base of the ovary contacts the rigid style after forcing down the hinged, bowl-like apical appendage of the keel. In *P. paucifolia* this is crested and perhaps acts as a landing pad. Pollen accumulated on the horizontal surface at the end of the style is deposited on the underside of the insect, which leaves behind foreign pollen obtained from previously visited flowers.

Outgrowths at the micropylar end of the ovule, usually termed "arils," but perhaps more properly called arillodes (see L. van der Pijl, Acta Bot. Neerl. 6: 618-641. 1957), since they develop from tissues of the outer integument (Bresinsky), not from either the funiculus or the hilum, may be of diagnostic size and shape in certain species. These two- or three-lobed structures, often composed of large, hyaline cells, are said to be important in local dispersal by ants that utilize their contents as a food source (Ridley).

Chromosome numbers have been reported for relatively few species of *Polygala*. Because few pollen mother cells are formed in each anther and the chromosomes are small and often numerous, good meiotic figures are hard to obtain. Other counting difficulties arise during meiosis which is characterized by a prolongation of prophase I and rapid completion of the stages between prometaphase I and telophase I and of the phases of meiosis II (Lewis & Davis). Speciation through polyploidy, aneuploidy, and perhaps hybridization is suggested by the reported chromosome numbers: $2n = 14, 16, 18, 24, 28, 30, 32, 34, 36, 38, 40, 42, 44, 46, 48, 52, 56, 68, 72, \text{ca. } 84, 96, \text{ and } 104-108$, with $2n = 34$ being the most frequently obtained count (9 spp.).

The genus is of little commercial importance. Several species, includ-

ing *Polygala myrtifolia* L., from South Africa, *P. paucifolia*, and *P. Chamaebuxus*, are sometimes cultivated as ornamentals, and preparations containing saponins from the thick, fleshy root of *P. Senega* are used medicinally as expectorants for treatment of various forms of bronchitis and asthma. Until recently, most senega root came from Manitoba and Saskatchewan, Canada (Gillett). The species is cultivated in Japan and India for its roots; elsewhere naturally occurring stands are harvested. *Polygala butyracea* Heck., from tropical Africa, is reported to be a source of fiber used locally for making cloth and other items (Hutchinson).

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EMBRYOLOGY OF THE MAGNOLIALES AND
COMMENTS ON THEIR RELATIONSHIPS¹

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COMMENTS ON FAMILIES

Austrobaileyaceae. The genus *Austrobaileya* has been included in Magnoliaceae (White, 1933), in Austrobaileyae, as a subfamily of the Dilleniaceae (Croizat, 1940), Monimiaceae (see Bailey & Swamy, 1949), or as a separate family Austrobaileyaceae (Croizat, 1943). According to Bailey and Swamy (1949) the presence of monocolpate pollen, ethereal oil cells, and absence of raphides negate any relationship with the Dilleniaceae. Since this genus has unilacunar nodes, it falls in category A of dicotyledonous families of Bailey and Swamy (1950) and thus has no close affinities with the Magnoliaceae. Bailey and Swamy (1949) remarked that the totality of evidence provides no justification for excluding *Austrobaileya* from Monimiaceae unless the concept of the family is narrowed to exclude such genera as *Trimenia*, *Piptocalyx*, and *Amborella* (see also Bailey & Swamy, 1948). However, in a subsequent paper discussing the relationships of the Monimiaceae (Bailey & Swamy, 1950) they include this genus in a distinct family, the Austrobaileyaceae, closely related to Monimiaceae.

Magnoliaceae, Degeneriaceae, and Annonaceae. Previously the Magnoliaceae included a number of genera of doubtful affinities like *Drimys*, *Schisandra*, *Illicium*, *Trochodendron*, *Tetracentron*, and *Euptelea* (see Bentham & Hooker, 1862-67; Engler & Prantl, 1887-1909; Hutchinson, 1959; Rendle, 1952). Dandy (1927) has circumscribed the family to include ten genera. Kapil and Bhandari (1964) have compared morphological and embryological characters of Magnoliaceae, *Schisandra*, and Illiciaceae and supported the removal of *Schisandra* and its allies to Schisandraceae, and *Illicium* to Illiciaceae (see also Bailey & Nast, 1948; Gifford, 1950; Lemesle, 1955; Ozenda, 1946; Smith, 1947). *Drimys* has also been rightly removed to a separate family, the Winteraceae (Bhandari, 1963; Bhandari & Venkataraman, 1968; Dandy, 1933; Smith, 1942, 1943; Van Tieghem, 1900). Similarly the removal of *Trochodendron* and *Tetracentron* (Bailey & Nast, 1945; Croizat, 1947; Nast & Bailey, 1945, 1946; Smith, 1945) and *Euptelea* (Lemesle, 1946; Nast & Bailey, 1946; Smith, 1946) to their representative family has been amply justified. The above conclusions are also corroborated by pollen morphology (Erdtman, 1952).

The family Degeneriaceae was established by Bailey and Smith (1942) and has been recognized as a distinct family of the magnolian stock (see

¹Continued from volume 52, p. 39.

Eames, 1961), closely related to the Magnoliaceae and Himantandraceae (Bailey, Nast, & Smith, 1943; Swamy, 1949). Hutchinson (1959), however, considers that *Degeneria* is closely related to *Exospermum* and *Zygo-gynum* and should, therefore, be included in the Winteraceae. Bhandari (1963) has compared the morphological and embryological features of the Winteraceae and Degeneriaceae, and remarked “. . . *Degeneria* differs from the Winteraceae in many important features like the perianth, stamens, pollen grains, endosperm, embryo, seed coat and floral and vegetative anatomy, and is therefore, rightly placed in a separate monogeneric family, the Degeneriaceae (Bailey and Smith, 1942).” Swamy (1949) has concluded that Degeneriaceae, Himantandraceae, and Magnoliaceae are distinct but closely related families.

Bailey *et al.* (1943), Bailey and Smith (1942) and Swamy (1949) have pointed out that Magnoliaceae, Himantandraceae and Degeneriaceae are closely related. Eames (1961), however, maintains that the Annonaceae are most closely related to the Magnoliaceae and the two are perhaps derived from the same ancestral stock, whereas Eupomatiaceae, Himantandraceae, and Degeneriaceae are other families having affinities with the Magnoliaceae. In the absence of any embryological literature on the first two families Kapil and Bhandari (1964) have compared embryological, morphological, and anatomical features of the Magnoliaceae, Degeneriaceae, and Annonaceae and concluded that these families possess many common features such as the tree habit; multilacunar node; bisexual flowers (rarely unisexual in Magnoliaceae); embedded microsporangia; glandular tapetum with binucleate cells; monocolpate pollen (occasionally acolpate in Annonaceae) in which the generative cell is cut off towards the distal end; anatropous, bitegmic, and crassinucellate ovules; Polygonum type of embryo sac with ephemeral antipodal cells; cellular endosperm and follicular fruits. All these features strongly indicate their close relationship. At the same time they differ from each other in some important characters. The stamens are 1-traced in Annonaceae, 3-traced in Degeneriaceae and 3–7-traced in Magnoliaceae. In Magnoliaceae microspores are released from tetrads soon after their formation while they are retained in the tetrad till the differentiation of exine and colpi in the Degeneriaceae and in permanent tetrads in some members of Annonaceae; Ubisch granules are present in Magnoliaceae and not in the other two; the endosperm is ruminant in Degeneriaceae and Annonaceae but not in Magnoliaceae; sarcotesta is present in Magnoliaceae and Degeneriaceae but is absent in Annonaceae; instead a fleshy aril is found which is absent both in the Magnoliaceae and Degeneriaceae; follicles open by a dorsal suture in Magnoliaceae, by a ventral suture in Degeneriaceae, while in Annonaceae follicles become syncarpous in the fruit. The three families differ also in having varied basic chromosome numbers. In Magnoliaceae it is $n = 19$; in Degeneriaceae $n = 12$, while in Annonaceae it varies from $n = 7, 8, \text{ or } 9$. The family Himantandraceae resembles Degeneriaceae however, in possessing $n = 12$. It is therefore, quite evident that although these families are closely related they cannot be arranged in a linear phylogenetic sequence. They

have some features common to all, others overlapping with either of the families, and still others unique to each one. It may be concluded that they are closely related but distinct families of the magnolian complex.

Winteraceae. Bentham and Hooker (1862-67) recognized one genus *Drimys*, and along with *Illicium* placed it in the tribe Winterae of the Magnoliaceae. Van Tieghem's (1900) was the first extensive survey of the family. He proposed the group Homoxylées to include all the vesselless dicotyledons and Drimyacées to comprise the five genera. *Pseudowintera*, the sixth genus, was added to the Winteraceae by Dandy (1933).

The Winteraceae have unique features such as the trends of specialization of the conduplicate carpel; the primitive stamen; permanent tetrads (elsewhere present only in the Lactoridaceae and Annonaceae) with pollen having the generative cell cut off towards the proximal face; extensive fibrous endothecium, monoporate pollen with conspicuous to minute reticulations; phenolic compounds in the outer epidermis of the outer integument; distinctive endosperm, embryo, and seed structure (*see also* Bailey & Nast, 1945).

Smith (1943a,b), however, agreed with Burt (1938) in transferring *Tetralthalamus montana* from the Guttiferae but merged this genus with *Bubbia* as *B. montana* and therefore, recognized only six genera in the Winteraceae. Hutchinson (1959) and Barkley (1966) consider *Tetralthalamus* to be deserving of generic rank and the latter author further favors the recognition of *Wintera* and *Lassonia* (= *Magnolia*, *see* Willis, 1966) as winteraceous genera. Hutchinson (1959) is of the opinion that *Degeneria*, the monotypic genus of the Degeneriaceae (Bailey & Smith, 1942), is closely related to *Exospermum* and *Zygogynum* and should also be included in the Winteraceae.

Embryological information for *Tetralthalamus*, *Lassonia* and *Wintera* is lacking and therefore, any discussion pertaining to the taxonomic placement and relationship of these genera must await such data. Bhandari (1963) and Bhandari and Venkataraman (1968) have shown that *Degeneria* differs (Swamy, 1949) from the Winteraceae in many important aspects such as the perianth, stamens, pollen grains, endosperm, embryo, seed coat, and floral and vegetative anatomy, and they support Bailey and Smith (1942) in thinking this genus is rightly placed in a separate family, the Degeneriaceae, and deny any close affinities with the Winteraceae. Bhandari and Venkataraman (1968) considered that *Illicium* differs from the Winteraceae in having vessels in the xylem; unilacunar node; no differentiation in calyx and corolla; endothecium not extending towards the connective tissue; 2-layered glandular tapetum; pollen grains shedding individually, tricolpate pollen; closed sessile carpel; ephemeral antipodal cells; Asterad type of embryogeny; and seed structure. These dissimilarities obviously preclude any possibility of Winteraceae being related to *Illicium* and justify its separation to Illiciaceae (*see also* Bailey & Nast, 1945; Erdtman, 1952).

Cytologically also the family is distinct. The basic number $x = 13$ in the species of *Drimys* section TASMANIA is similar only to that of *Illicium*

floridanum which is however of secondary origin by aneuploidy. No such evidence is available in Winteraceae. Secondly, the section *WINTERA* of *Drimys* and *Pseudowintera* have $n = 43$.

Taking into consideration the sum total of evidence from morphology, vegetative and floral anatomy (Bailey, 1944; Bailey & Nast, 1943a,b; 1944a,b; 1945; Nast, 1944), and embryology (Bhandari, 1963; Bhandari & Venkataraman, 1968; Sampson, 1963; Swamy, 1952), the Winteraceae form a distinct family of magnolian alliance but not closely related to any other existing family.

Myristicaceae and Canellaceae. The Myristicaceae is a homogeneous taxonomic unit. Because of the meager embryological information, not very dependable conclusions can be drawn. Joshi (1946), however, considers that the family is related to Annonaceae, and perhaps the ruminant endosperm and arillate seeds add further support to this conclusion.

The family Canellaceae has also been placed in either Parietales along with Violaceae, Bixaceae, Flacourtiaceae and Koeberliniaceae or in the woody Ranales near Myristicaceae, Illiciaceae, Schisandraceae, and Eupomatiaceae (Engler, 1964; Hutchinson, 1959). Wilson (1960) in a comparative study of wood anatomy concluded that the family is nearly related to Eupteleaceae, Eupomatiaceae, Illiciaceae, and Schisandraceae. Bessey (1915), Vestal (1935), and Wettstein (1935) regarded the families Myristicaceae and Canellaceae as closely related. Although the two families have a number of differences they also possess certain common features such as the simultaneous cytokinesis in the microspore mother cells; the generative cell cut off towards the proximal pole; anatropous, bitegmic, and crassinucellate ovules; Polygonum type embryo sac; ruminant endosperm; paratracheal parenchyma; and uniseriate rays. In both families the rays flare out in the phloem region. Parameswaran (1962) concluded that these two families have a greater degree of resemblance than the remaining families which possess ethereal oil cells, monocolpate pollen, and trilacunar nodes. However, one family cannot be derived from the other. Probably they had a common ancestral stock from which they deviated unidirectionally.

Schisandraceae and Illiciaceae. Most taxonomists, such as Bentham and Hooker (1862–1883), Engler and Prantl (1889–1897), and Rendle (1952) included *Schisandra* and *Kadsura* in a tribe, Schisandreae or a subfamily, Schisandroideae, of the Magnoliaceae. McLaughlin (1933), Whitaker (1933), Lemesle (1945, 1955), Ozenda (1946), Smith (1947), and Bailey and Nast (1948), on the basis of morphology, wood anatomy, and chromosome number, have concluded that Schisandreae should be raised to family rank as the Schisandraceae. This suggestion has been accepted and incorporated in most taxonomic treatments as that of Lawrence (1951), Hutchinson (1959), and Takhtajan (1966), Thorne (1968), and Cronquist (1968). On the basis of a comparative analysis of morphology, embryological and nodal structure of the Magnoliaceae, *Schisandra*, and Illiciaceae, Kapil and Bhandari (1964) pointed out that Magnoliaceae differs from *Schisandra* and Illiciaceae in having undifferentiated stamens with

1 to 7 traces and embedded microsporangia; bilayered glandular tapetum with binucleate cells; Ubisch granules; monocolpate pollen with smooth exine; unilocular ovary with 2 to 6 ovules; vascularized outer integument; testa differentiated into outer fleshy and inner stony regions; multilacunar and multitraced node; stipulate leaves; and $n = 19$ as the basic chromosome number; and supported the exclusion of *Schisandra* and *Kadsura* to their respective families (*see also* Kapil & Jalan, 1964). Bhandari and Venkataraman (1968) have shown that embryologically *Illicium* has no affinities with *Drimys* (*see also* Winteraceae) with which it was associated in the tribe Magnolieae of the Magnoliaceae (Bentham & Hooker, 1862–1868).

Kapil and Jalan (1964) evaluated the morphological, anatomical and embryological features of the Schisandraceae and Illiciaceae. The Schisandraceae possess the following characters in contrast to Illiciaceae: (a) climbers *vs.* trees or shrubs, (b) eustelic stem with well developed pericycle *vs.* pseudosiphonostele with poorly developed pericycle, (c) 3-traced unilacunar *vs.* 1-traced unilacunar node, (d) alternate leaves *vs.* pseudovercillate, (e) haplocheilic stomata *vs.* syndetocheilic, (f) non-pitted sclereids with crystals *vs.* pitted sclereids without crystals, (g) unisexual *vs.* bisexual flowers, (h) spirally arranged carpels without style *vs.* whorled carpels with style, (i) stamens monadelphous *vs.* stamens free, (j) hexacolpate *vs.* tricolpate pollen, (k) embryo sac Polygonum, Oenothera or modified bisporic (*see* Swamy, 1964) type *vs.* Polygonum type, (l) Onagrad type of embryogeny *vs.* Asterad type, and (m) fruit a berry with succulent pericarp *vs.* fruit a follicle with sclerotic pericarp. They (Kapil & Jalan, 1964) concluded that these two families deviate in a large number of characters and there seems to be no close relationship between the Schisandraceae and Illiciaceae as suggested by Whitaker (1933), Smith (1947), and Bailey and Nast (1948). Eames (1961) proposes that Schisandraceae and Illiciaceae, though more specialized, are closely related to the Magnoliaceae and it is possible that all three families probably have been derived from a common ancestral stock. On the other hand, Smith (1947) remarked that *Illicium* has no close allies other than *Schisandra* and *Kadsura*; a conclusion corroborated by the chromosome number of $n = 14$. At the same time he emphasized that the two groups have specialized along different lines and have retained certain primitive features. It is impossible to indicate which is the more primitive. Smith's remarks made about two decades ago, and those of Eames (1961), and Bailey and Nast (1948) seem unfounded in the light of embryological investigations carried out recently. Further, the recent evidence from the karyotypic analysis for Illiciaceae (Stone & Freeman, 1968) and Schisandraceae (Stone, 1968) clearly indicates that Schisandraceae differs from Illiciaceae in having a nearly symmetrical karyotype and lacking subterminal chromosomes. It may very well be that Schisandraceae and Illiciaceae again represent the relics of the extant magnoliales much like many other families such as Winteraceae, Eupteleaceae, and Lactoridaceae.

Monimiaceae and allies. The Monimiaceae *sensu lato* included a large

number of genera having doubtful affinities such as *Amborella*, *Austrobaileya*, *Idenburgia*, *Scyphostegia*, *Trimenia*, *Piptocalyx*, *Calycanthus*, and *Gomortega* (see Money, Bailey, & Swamy, 1950).

According to Money *et al.* (1950) *Amborella* has characters resembling those of members of the Monimiaceae such as spiral arrangement of leaves, bracteoles, and tepals; the form and vascularization of the carpels; pollen morphology; fruit morphology; absence of ethereal oil cells; presence of multicellular hairs and hippocrepiform sclereids; and absence of pericyclic fibers in the stem. However, it differs in the orientation of anatropous ovules, narrow rays, and a single arc-shaped leaf trace. Therefore, its position in Amborellaceae, closely related to Monimiaceae, is justified (see also Bailey & Swamy, 1948).

Similarly *Trimenia* and *Piptocalyx* have been removed to a separate family, Trimeniaceae, *Gomortega* to Gomortegaceae, *Calycanthus* to Calycanthaceae and *Austrobaileya* to Austrobaileyaceae and all of these families are interrelated (Bailey & Swamy, 1940, 1949, 1950).

Embryological information on Amborellaceae, Trimeniaceae, and Gomortegaceae is not available, and the embryological literature on Monimiaceae itself is not sufficiently extensive to draw dependable conclusions. However, the Monimiaceae, Calycanthaceae, and Hernandiaceae resemble each other in having the successive type of cytokinesis in the microspore mother cells; periplasmodial tapetum (occasionally glandular in Monimiaceae); anatropous, bitegmic (also unitegmic in Monimiaceae), and crassinucellate ovules; the massive parietal tissue formed by both the primary parietal cell and the nucellar epidermis; multicelled archesporium and functioning of numerous megaspore mother cells; Polygonum type of female gametophyte; and multiple embryo sacs. Such features indicate that these are closely related and form a compact group. As shown by Sastri (1963), all these families also possess affinities with Lauraceae and perhaps with the Lauralian line of Eames (1961), and the theory that they might have had their origin from a common ancestry seems justified. Money *et al.* (1950) also included these families in their group having monocolpate or its derived forms of pollen grains, ethereal oil cells, and unilacunar nodes.

Lauraceae. The Lauraceae are relatively advanced over other Magnolian families, and Eames (1961) recognized two phylogenetic lines within the Ranales *sensu lato*, the magnolian line and the lauralian line, the latter including families such as Lauraceae, Hernandiaceae, Myristicaceae, Monimiaceae, and Gomortegaceae. Sastri (1963) has evaluated critically the morphological and embryological data and concluded that Hernandiaceae resembles Lauraceae in having unisexual flowers; stamens with 2-celled anthers and a glandular appendage with vascular supply; periplasmodial tapetum; successive type of cytokinesis; acolpate, 2-celled pollen; two-traced carpel; single anatropous ovule, and similar structure of the seed coat and pericarp; and that therefore, the two families are closely related (see also Shutts, 1960). Similarly Calycanthaceae are closely related to Lauraceae in having periplasmodial tapetum; multinucleate tape-